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Original Research Article

Long lasting impressions: After decades of regeneration rainforest biodiversity remains differentially affected following selective logging and clearance for agriculture

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ABSTRACT

The need to complement primary forest protection with the conservation of regenerating tropical forest is becoming increasingly well-understood. However, the persistence of biodiversity differences between areas once subjected to different anthropogenic land-uses, after long periods of regeneration, remains poorly understood. We investigate long-term differences in species richness, diversity, relative abundance and community evenness within a regenerating rainforest previously subjected to two different but common types of human disturbance: selective logging and clear-felling for agriculture. Even after a 30 year recovery period, and despite close-proximity to protected primary forest that provided favourable recolonization potential, species richness and diversity of amphibians, butterflies, understorey birds and nocturnal birds were all lower in post-agriculture secondary forest, compared to regenerating selectively logged forest; in contrast, mammals showed no significant difference. Species richness in secondary forest was on average $18 \pm 6.7\%$ lower, and diversity was $13 \pm 7.6\%$ lower than in the selectively logged forest. Community evenness and relative abundances also displayed differences related to historic human disturbance type. However, the measured difference in species richness (18%) between selectively logged and secondary forest was 60% smaller than previous indirect comparisons based on young areas of regenerating forests have suggested. We find that human-induced differences in tropical biodiversity are long lasting but also suggest that even historically highly disturbed regenerating tropical forests could, with appropriate management, provide important opportunities for conserving tropical forest biodiversity.

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1. Introduction

Despite growing awareness of the potential value of regenerating tropical forest following clearance or logging, recent reviews have suggested contradictory conclusions on the biodiversity value of such forest. Even within logged forest specifically, some conclude that "most biodiversity can be retained in tropical forest impacted by logging" (Edwards et al., 2014; Putz et al., 2012), whereas others suggest that even relatively low levels of selective logging and habitat clearance can "halve the levels of species richness" (Burivalova et al., 2014). Burivalova et al. (2014) conducted a meta-analysis on data from 48 tropical studies and concluded that as selective logging intensity increased, species richness was heavily reduced, with amphibian and mammal species richness below 50% of primary forest levels in some cases. Gibson et al. (2011) suggest that selectively logged forest showed limited ecological disruption and biodiversity loss, but that other areas of forest regenerating following greater levels of clearance for agricultural uses (secondary forests) had limited potential for preserving biodiversity. Chazdon et al. (2009a) showed a range between studies of 33–86% of primary forest species detected within regenerating secondary forests. There is wide variation in the terminology used as labels for such disturbed tropical forest systems, so in this study we follow the terminology suggested by Putz et al. (2012); using 'secondary forest' for forest re-growing on abandoned agricultural land that was previously forest, and 'logged forest' for disturbed primary forest regenerating following selective logging.

It is an acknowledged feature of the literature that very few studies have been carried out at a within-site scale that directly compares differences in biodiversity patterns between selectively logged and secondary tropical forest (Dunn, 2004; Bowen et al., 2007; Dent and Wright, 2009). Dunn (2004) showed that just two of 34 studies assessed more than a single type of forest disturbance within a site. Bowen et al. (2007) reviewed 68 studies to investigate faunal recovery in regenerating forests from a global perspective. Just two of these were found to directly compare faunal communities following different forms of forest clearance. Dent and Wright (2009) reviewed 65 studies across 114 regenerating forest sites and emphasised the importance of understanding different types of disturbance history by categorising forests into four different prior land-uses; but again, the studies available in this literature are dominated by between-site comparisons because of the lack of direct within-site comparisons that control for other potential between-site differences (such as differences in climate, topography and ongoing disturbance levels).

Another common feature in biodiversity assessments of tropical forest after disturbance are studies based upon assessments of sites still undergoing human impacts (Anand et al., 2010; Barlow et al., 2007; Dent and Wright, 2009; Gibson et al., 2011; Norris et al., 2010), such as hunting or logging. On-going impacts have the potential to magnify initial biodiversity impacts and limit its recovery (Barlow et al., 2016; Burivalova et al., 2014; Roldán and Simonetti, 2001; Urquiza-Haas et al., 2011) in ways which may confound assessments of the biodiversity and conservation potential of regenerating forest biodiversity. The contradictory nature of this literature and the findings on which it is based suggests little scientific consensus on the biodiversity and conservation value of regenerating secondary and regenerating primary forests disturbed by selective logging (Sloan et al., 2015).

This low frequency of direct comparisons, in the absence of on-going effects, is potentially problematic for answering a key question for developing tropical forest conservation strategies: if resources were to be invested in their conservation, how different would the future biodiversity conservation value of regenerating secondary forest be compared to forest regenerating after selective logging? Without using direct within-site comparisons, potential between-site differences (other than disturbance history prior to forest regeneration) cannot be properly controlled for, and measured differences between disturbance types are correlational in nature. In such situations, inferring that differences in disturbance history have had a causative effect is problematic. With indirect comparisons, if on average regenerating secondary forests that were once cleared for agriculture are growing on sites that are closer to human populations or allow greater human access, they are therefore also more likely to suffer higher ongoing disturbance levels. In such cases, the differences in biodiversity values between secondary forest and selectively logged forest are likely to be caused by the ongoing disturbance, as well as the nature of the original disturbance, and the causative contribution of each will be hard to disentangle.

Also evident in the comprehensive review by Dent and Wright (2009) is that a large proportion of the study sites are young regenerating forests, with 65 sites (57%) of an age <21 years since abandonment. This is true for many reviews (Anand et al., 2010; Barlow et al., 2007; Chazdon et al., 2009a; Gibson et al., 2011; Irwin et al., 2010; Letcher and Chazdon, 2009; Norris et al., 2010; Sodhi et al., 2010; Tabarelli et al., 2010), where the types of regenerating forest evaluated are often relatively young (<15 years). Although short time scales are useful for understanding the impacts on biodiversity of recent change, if the aim is to assess the future value regenerating rainforest may have for conservation, then direct comparisons in older regenerating forest would be preferable (Chazdon et al., 2009b).

Therefore, the goal of this study was to directly compare for multiple taxa (in the absence of the potentially confounding effects of young age of regeneration and on-going human disturbance) how differences in historic human disturbance might influence current biodiversity patterns (species richness, diversity, encounter rates and community evenness) of secondary versus selectively logged forest. This case study sought to answer three key questions: 1) To what extent do differences in biodiversity patterns within regenerating forest, once subjected to different types of historic disturbance (selective logging vs. clearance for agriculture), still exist 30 years after these disturbances ended? 2) Do different taxonomic groups show the same response patterns to the different types of historic disturbance in an older regenerating forest, consisting of both secondary and selectively logged forest? 3) When controlling for potential external confounding factors by making within site

comparisons, are measured differences between secondary and selectively logged regenerating forests comparable in size to values generated based on earlier, more indirect comparisons?

2. Methods

2.1. Choice of study site

The regenerating rainforest selected for this study, the Manu Learning Centre (MLC), was located in close proximity to a large protected area network providing source populations for recolonizing the forest as it regenerated (see Whitworth et al., 2016a, b). The MLC is situated within the Manu Biosphere Reserve, a UNESCO World Heritage Site designated to protect the globally important Amazon rainforest in and around Manu National Park, SE Peru (Fig. S1). The biosphere reserve consists of core protected areas surrounded by buffer zones with historically high human impact, including extensive logging and clearance for subsistence agriculture.

Key features of the study site were: 1. a known history of different anthropogenic disturbance types within a small area, allowing within-site comparisons of effects in the absence of potential landscape level differences between study sites. The disturbance types included selective logging (regenerating selectively logged forest; ~332ha), an area of complete clearance for conversion to intensive agriculture for coffee and cacao (regenerating secondary forest; ~293ha), and a mixed area between the two disturbance types that once consisted of a mosaic of completely cleared and selectively logged areas through partial clearance for agriculture (mixed disturbance regenerating forest; ~183ha) (n.b. the nearest undisturbed primary forest that we could have accessed for surveys was ~80 km away and at a lower elevation of ~300 m asl compared to 460 m asl at the study site). We considered this to be unsuitable for disentangling any potential differences in disturbance history, from those related to differences in elevation, soil type, climate and topography; see Bowen et al. (2007). This did not impact the aims of this study, as we are aiming to compare different types of disturbed forest rather than compare disturbed forest to primary forest; 2. the site had been strictly protected from hunting and other human impacts since 2002 by the presence of the MLC, allowing on-going human disturbance to be excluded as a causal effect; 3. the conservation investment at the site hasn't differed significantly between secondary forest and selectively logged disturbance types, another factor that is being controlled for by working with a single site; 4. the site has had a long period for regeneration since disturbance events. Disturbances to the site occurred during the 1960s-1980s and the study site has had at least 30 years of regeneration time, so at the time of the study the whole area was covered by closed canopy forest.

As such, this was an ideal site to investigate the potential biodiversity and conservation value of a “best-case scenario” (see Whitworth et al., 2016a) for regenerating rainforest, in the absence of confounding effects of on-going non-natural disturbance. We therefore expected that the differences in species richness, encounter rates of species and community structure between locations within the two different regenerating types (secondary vs. selectively logged forest) might be negligible given their close proximity to protected areas that allowed for the dispersal of old growth species and given the relatively long time frame since disturbance. Although plant species turnover may still be high within a small area such as our study site, the groups we study are mobile vertebrates and invertebrates, and over the 30 year time scale we consider here, there would be no barrier to the species being found anywhere in the 800ha of the study site. Therefore, in the absence of an effect of disturbance history, we would expect the species to be randomly distributed with respect to the disturbance history of sampling locations.

2.2. Habitat classification

Initially, the boundaries between habitats with different disturbance histories were identified by two of the authors visiting the site to visually inspect it and record distinct points of transition between the forest types. These boundaries were then confirmed by consulting local guides who had expert local knowledge related to the specific historic land-use of the study site. Both approaches identified consistent points that were marked as the boundaries of the different disturbance histories. To confirm if these identified boundaries related to current differences in forest structure, vegetation data relating to 12 different measures of forest structure were collected across 571 sampling locations. A factor analysis was performed to reduce these variables using Minitab v.14.12, then the factor scores mapped using a kriging feature in ArcGIS. In order to verify the statistical difference of factor scores between assigned habitat areas, an analysis of variance analysis (ANOVA) was carried out (see Appendix S1 to S4 and Fig. S2). To assess the floristic composition in each disturbance type, 10 2 $\times$ 50 m plots (0.1ha Gentry plot) were carried out (for detailed methodology, see Phillips and Miller, 2002).

2.3. Faunal study groups

This study measured the biodiversity of four key taxonomic groups (amphibians, birds, butterflies and medium-large terrestrial mammals), chosen because they are of well-known conservation importance and provide numerous ecosystem functions (Banks-Leite et al., 2010; Beck et al., 2010; Cassano et al., 2012; Eigenbrod et al., 2008; Goyette et al., 2011; Hamer et al., 2003; Hayes et al., 2010; Horner-Devine et al., 2003; Salvador et al., 2011; Sberze et al., 2010; Whitworth et al., 2015).

2.4. Study approach and survey methodologies summary

The study aimed to assess how biodiversity was distributed across different human-disturbed rainforest types following a long period of regeneration. Using a small spatial scale (~800ha) allowed us to avoid confounding effects of large scale drivers of spatial auto-correlation, such as climatic or geographic differences. With an absence of any significant geographic barriers (e.g. large rivers or mountains) to hinder species dispersing across the site, we predicted that in the absence of any effects of differences in historic disturbance, biodiversity would be distributed randomly across the study area. If human disturbance history differentially impacted biodiversity, we predicted that we would find differences between locations once subjected to different forms of disturbance. Survey locations for all groups had similar although not identical levels of survey effort due to weather and logistic constraints, as some survey sites were first installed during 2012 and additional sites were installed in the 2013 field season. Any differences in survey effort were balanced across all of the disturbance types, and would therefore not be expected to influence the patterns identified (see Table S1). We accounted for any potential differences in survey effort within the analysis by creating extrapolated accumulation curves to represent equal numbers of detections and verify that patterns in the observed data are congruent with these projections. As a final check, models were run with survey effort added as a co-variant, but these showed no overall impact of sample size. The amount of variation explained only increased consistently for amphibians, and in this case, there was no effect on the patterns of the main variable effects, so we concluded that the sample size differences were not sufficient to influence the effects observed.

Amphibians were surveyed nocturnally through visual encounter surveys (Beirne et al., 2013) at 12 locations within the study site. Morning line transects were conducted to survey the overall diurnal bird community, with a total of total 33 transect survey locations walked throughout the study site to monitor all bird species both visually and by call (Bibby et al., 2000). Understorey birds were surveyed across 18 locations using mist nets. Nocturnal birds were surveyed by call along 37 line transects. Butterflies were surveyed across 18 locations, using Van Someren-Rydon traps (Hughes et al., 1998). Mammals were surveyed across nine camera trap locations. Terrestrial medium to large mammals were the target group for the analysis, therefore excluding arboreal species, small rodents and most aquatic species (Tobler et al., 2008). See Appendix S5 for detailed descriptions of survey methods and Fig. S3 for survey location maps.

2.5. Biodiversity analysis

In order to investigate differences in biodiversity distribution between disturbance types, we assessed a number of frequently used biodiversity metrics (Bruton et al., 2013; Hu et al., 2013). To assess observed species richness levels and the extent to which our effort had detected as many species as are likely to be found within each disturbance type, we created rarefaction curves using the Rich package (Rossi, 2011) and plotted them using program R (R Core Team., 2012). Where sampling effort provided fewer individual detections in one type, we used Estimate S (Colwell, 2006) to extrapolate the lower lying curve towards an equal number of individual detections for a clearer comparison of richness levels (Colwell et al., 2012). Three estimators of species richness were calculated for all survey groups (Gotelli and Colwell, 2011). The three estimators, Jack 1, Chao 2 and Mmmeans, have previously been shown to provide effective estimates for birds, butterflies or mammals (Fermon et al., 2005; Herzog et al., 2002; Hughes et al., 2002; Ramesh et al., 2010; Tobler et al., 2008), while the most effective estimators for amphibians remain unresolved (Veith et al., 2004). The average of the above three estimators was calculated for each group across each disturbance type (note that the Chao 2 result for mammals was excluded from the calculated average as Tobler et al. (2008) suggest this to be a poor estimator for camera traps and our estimates here displayed (potentially) exaggerated levels). Following the recommendations of Altman and Bland (2011) and Gotelli and Colwell (2011), to assess significance of any differences in richness, estimated 84% confidence intervals for the average estimated species richness were calculated for each group in secondary and selectively logged forest. When comparing two confidence intervals, no overlap at the 84% confidence interval level indicates a statistically significant difference at $p=<0.05$. In contrast, two non-overlapping 95% confidence intervals are indicative of considerably lower p values.

Species diversity was defined as the Shannon diversity index (Seshadri, 2014; Trimble and Aarde, 2014). Repeating the analyses using Fisher's Alpha, Simpson and Shannon Exponential diversity indices did not change the pattern of results significantly and therefore are not presented (see Fig. S4). All richness and diversity estimators were calculated in Estimate S (Colwell, 2006).

As we were investigating what was effectively a natural experiment (or a comparison between two non-designed treatments) and not human designed one, it was not possible to intersperse independent sampling locations as a simple way to demonstrate treatment replication (in addition to the sampling replication described in the survey methods). Therefore, analytical approaches were used to confirm independence of sampling locations. It has been highlighted that many tropical forest studies investigating effects of human disturbance on biodiversity due to logging have the potential for pseudo-replication due to spatial auto-correlation (Ramage et al., 2013; in agreement with Hurlbert, 1984; Heffner et al., 1996). In this context, Ramage et al. (2013) suggest that whilst interspersion is a desired goal where human designed experiments are practical, other approaches such as investigation of natural experiments provide useful scientific evidence if causes of spatial variation, other than the “treatment” effect, are investigated and controlled for as necessary (see Davies and Gray, 2015). As such, pseudo-replication only occurs if the results are over generalised (Ramage et al., 2013). Therefore, following Ramage et al. (2013) recommendations, we included additional control variables in our analysis, utilised spatial statistics to

confirm the absence of spatial auto-correlation and finally, considered the likelihood of alternative inferences from our results.

2.6. Statistical analysis

In order to investigate if differences in average estimated species richness indices and Shannon diversity between selectively logged, secondary and mixed disturbance survey locations were significant, a series of linear models were carried out. Having excluded potential large scale causes of spatial auto-correlation by focussing on a small scale study area over which large scale factors would not vary, we also considered if there were any consistent local scale differences between sampling locations ('altitude', 'slope extent' and 'distance to the main river' of each sampling location were included as covariates to control for any potentially confounding effects of these variables; see Appendix S6 for further details). Finally, to confirm that any potential spatial auto-correlation between survey locations had been controlled for in the analysis, a Moran's I test was carried out in program R (R Core Team., 2012) on the residuals of each model to test if there was any spatial auto-correlation that might lead to pseudo-replication (ape package; Paradis et al., 2004).

In order to determine if there was an overall difference in relative abundance across all faunal groups, we conducted an analysis of variance test (ANOVA) between locations with logged and cleared disturbance histories for each specific study group. We decided to test specifically logged and cleared disturbance habitats and exclude the mixed disturbance area from areas of the analysis so that the two different but common land-uses from the region could be compared more clearly. The mixed disturbance habitat represented a mixture of these disturbances and may be likely to harbour a higher proportion of transient species, being located directly between the other two disturbance areas (Beirne et al., 2013; Gardner et al., 2007b). In addition to testing overall groups, the relative encounter rates of indicator amphibians (Pearman, 1997) and birds (Stotz et al., 1996) were tested for differences between disturbance types.

Dominance-diversity (Whittaker) plots were produced and compared for all study groups to compare the evenness of community, across cleared and logged disturbance histories, using the vegan package (Oksanen et al., 2011) in program R (R Core Team., 2012). Significant differences in slope, and therefore significant differences in community evenness, were assessed through the use of a linear model with log relative abundance as the response term and an interaction between species rank and habitat type as continuous and categorical fixed effects, respectively. Species specific changes in abundance and rank of the five most abundant species from both selectively logged and secondary forest were labelled on the plots and assessed visually to note changes to species composition in terms of dominant species.

3. Results

3.1. Habitat classification

The habitat classification provided a clear separation between different disturbance types in terms of identifiable features related to overall forest structure. The ANOVA analysis between factor scores was statistically different between disturbance areas for the first three factors (Appendix S4), which agreed with patterns also observed from the kriging maps (Fig. S2). The tree species richness in selectively logged forest (SLR) was over double (60 species), and the number of tree families almost three times greater (31 families), than that of the secondary (CCR) habitat (29 species from 11 families; see Table S2 to S3). In general the selectively logged (SLR) habitat contains many large hardwood species (Meliaceae, Moraceae, Sapotaceae) while the secondary (CCR) forest contains smaller softwoods and palms (Melastomataceae, Rubiaceae and Arecaceae- Table S4).

3.2. Testing for alternative explanatory factors and spatial auto-correlation

Based on the general linear modelling, we concluded that within site differences in altitude, distance from the main river or slope intensity could not explain the observed differences in diversity and species richness, suggesting that differences observed were instead linked to the different types of historical disturbance. On only one occasion out of 20 general linear models did one of the more complex models display a lower AICc value than the disturbance history only models (Simpson diversity from diurnal bird transects – the model with an added habitat*altitude interaction had the lowest AIC value), and in this case the ΔAICc <2 (so this model was not better than the disturbance history only model, see Table S5). In 18 of the 19 models in which the AICc value was lowest for the disturbance history only models, a ΔAICc >2 was observed suggesting that disturbance history was the key factor in explaining differences in biodiversity. Testing of the model residuals showed no evidence of spatial auto-correlation between samples with very low correlations (range from −0.21 to 0.02) and non-significant observed Moran's I values (range from $p = 0.15$ to 0.99) for all groups and all response variables (see Table S6).

3.3. Species richness

Overall, secondary forest regenerating after complete clearance (CCR) was estimated to contain 18% ($\pm$6.7) fewer species than selectively logged forest regenerating after selective logging (SLR; see Table 1). Across all groups (with the exception of terrestrial mammals), the most general pattern is that selectively logged forest is the most species rich whilst secondary forest generally contains the lowest number of species (Fig. 1).

Table 1
Observed species richness and species richness estimates for rainforest with different disturbance histories. Based on six different survey methods targeting four taxonomic groups. Selectively logged forest = SLR, secondary growth = CCR and mixed disturbance area = MXD.

		Disturbance Type	Shannon diversity (standard deviation)	Observed Species Richness[a]	Extrapolated Species Richness[b]	Estimated Richness				Coverage (%)[d]	Completeness (%)[e]
						MMMean	*Jacknife 1*	*Chao 2*	Average[c]		
Amphibians	**Transects (x5 100m transects/ night)**	SLR	2.38 (0.01)	26	26	29	31	28	30	87	76
		CCR	2.32 (0.03)	19	21	24	24	20	23	83	56
		MX	2.15 (0.02)	22	28	25	31	28	30	74	65
		Total		34							
Birds	**Diurnal line transects (400m lengths)**	SLR	4.28 (0.01)	169	210	188	293	296	259	65	66
		CCR	4.21 (0.01)	177	177	185	252	221	219	81	69
		MXD	4.31 (0.01)	176	196	193	267	240	233	76	69
		Total		256							
	Mist-netting	SLR	3.9 (0.01)	86	86	120	116	112	116	74	70
		CCR	3.82 (0.02)	71	76	96	97	115	103	69	58
		MXD	3.79 (0.01)	77	77	102	106	116	108	71	63
		Total		123							
	Nocturnal line transects (500m lengths)	SLR	1.71 (0.02)	10	10	12	10	10	11	93	83
		CCR	1.1 (0.01)	6	6	6	7	6	6	92	50
		MXD	1.13 (0.02)	6	7	6	8	8	7	80	50
		Total		12							
Butterflies	**Baited traps**	SLR	4.19 (0.01)	143	143	166	178	170	171	83	80
		CCR	3.84 (0.01)	115	128	140	152	144	145	79	64
		MXD	3.9 (0.01)	120	135	146	159	161	155	77	67
		Total		179							
Mammals	**Camera traps**	SLR	2.42 (0.01)	21	23	23	25	(24)	24	88	91
		CCR	2.54 (0.01)	21	22	21	28	(42)	25	84	91
		MXD	2.64 (0.01)	20	20	21	22	(20)	22	91	87
		Total		23							

[a] Number of species observed.
[b] Number of species estimated when curves extrapolated to the same number of individuals (extrapolations made only equal to the disturbance history with the highest number of records or to a maximum of three times the number of observed individuals).
[c] Mean estimated species richness - 'classic Chao 2 was used in cases where CV > 0.5.
[d] Sampling coverage defined as:$^{b}/^{e}$*100.
[e] Number of species observed as a percentage of combined species across all habitats.

For the individual taxonomic groups, the average total species richness estimate for amphibians was higher in selectively logged regenerating forest (SLR) than secondary growth (CCR) forest (Table 1), with the selectively logged estimated to contain 29 species and secondary just 23 species (13% fewer than selectively logged - significant (at p=<0.05), based on no overlap between 84% confidence intervals for the final estimate). The average richness estimators from mist-net data predicted selectively logged forest to contain 116 species whilst secondary was estimated to hold 103 species (11% fewer than selectively logged - significantly different, with no overlap between 84% confidence intervals). The average richness estimates for diurnal bird transects predicted selectively logged forest to hold 248 species, whilst secondary is estimated to hold 223 species (10% fewer than selectively logged - not significant, with overlap between 84% confidence intervals). The average estimated species richness for nocturnal birds predicted selectively logged forest to contain 11 species, whilst secondary is estimated to hold 6 species (45% fewer species than selectively logged forest – significant, based on no overlap between 84% confidence intervals). The average estimated butterfly species richness was highest in selectively logged forest, containing 171 species and secondary growth just 145 species (15% fewer than selectively logged - significant, based on no overlap between 84% confidence intervals). The average species richness estimates of medium-large terrestrial mammals were similar, with 24 species being estimated in selectively logged and 25 in secondary forest. This difference did not appear to be significant, with overlap between 84% confidence intervals. Using the best fit disturbance only model for those groups with sufficient sampling locations, general linear models demonstrated that disturbance history was a useful predictor of estimated species richness, often explaining a large proportion of variation. For bird transects, disturbance history explained 13.2% of variation ($df = 22$, $F = 3.2$, $p = 0.089$); for birds captured in mist-nets, 43.7% of variation ($df = 5$, $F = 3.1$, $p = 0.153$); for butterflies, 52% of variation ($df = 11$, $F = 10.8$, $p = 0.008$) and for amphibians, 75.1% of variation ($df = 7$, $F = 18.1$, $p = 0.005$).

In terms of unique species between secondary and selectively logged forest, more unique species were detected for amphibians (13 vs.7), butterflies (50 vs. 22), birds caught in mist nets (39 vs. 24 and nocturnal birds (6 vs. 2; see Table S7 for species lists between selectively logged and secondary forest). Diurnal bird transects displayed more unique species in secondary forest than selectively logged forest (57 vs.49) and mammals showed the same number of unique species (2 per habitat type).

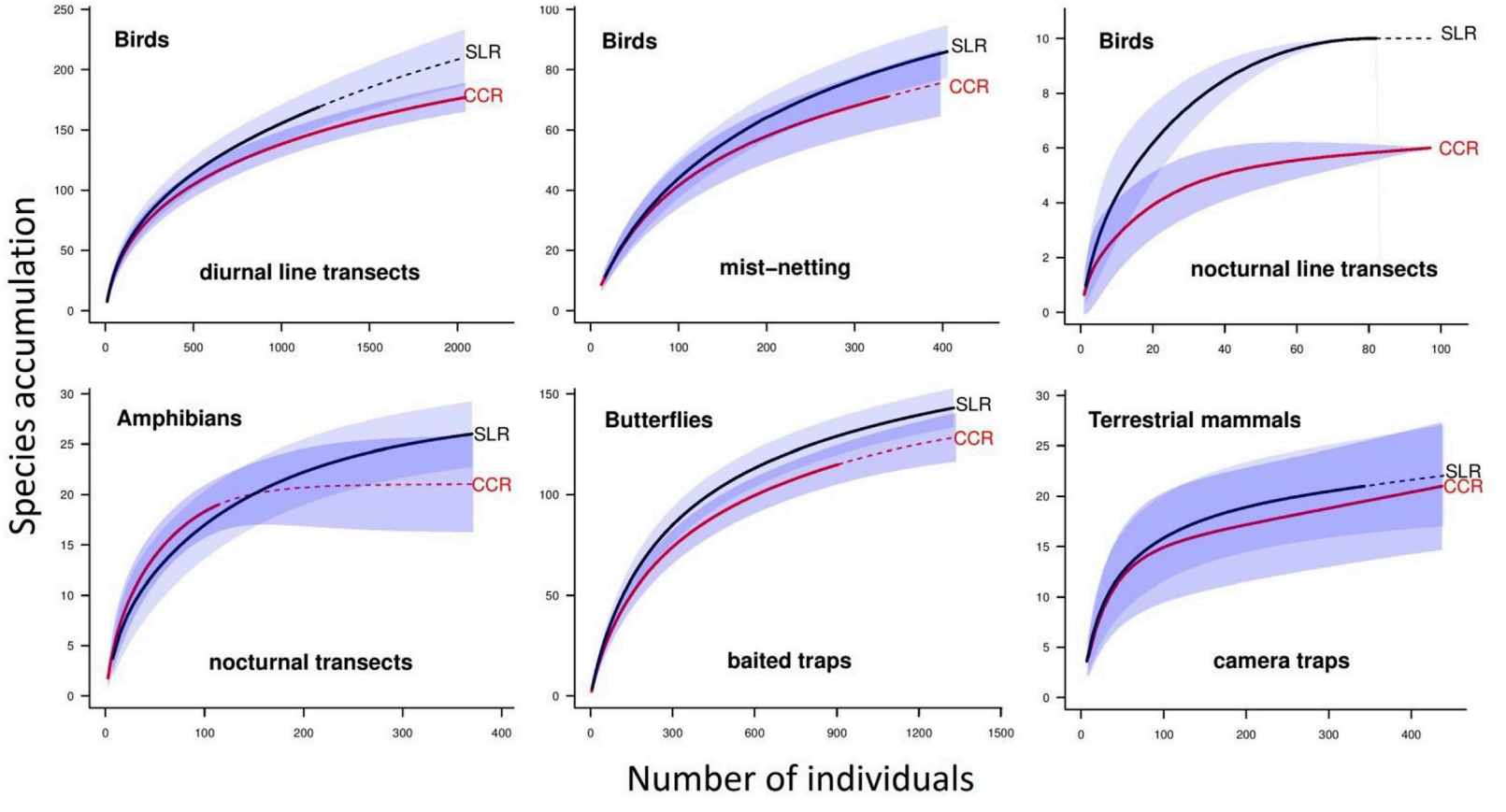

Fig. 1. Species accumulation curves for study groups across selectively logged (SLR) and secondary growth (CCR) disturbance types. Solid lines represent the observed number of individuals recorded and dashed lines represent projections for habitats with lower numbers of individuals sampled towards the same number of individual detections in other habitats. The shaded areas represent 95% confidence intervals.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Species diversity

In terms of species diversity, secondary forest (CCR) was on average 13% (±7.6) lower than selectively logged regenerating forest (SLR). The general pattern was that selectively logged forest was the most species diverse, whilst secondary forest generally held the lowest levels of species diversity (with the exception of mammals; see Fig. 2). The general linear modelling showed that disturbance history as a predictor of diversity explained 10.3% of variation in birds surveyed by transects ($df = 22$, $F = 2.4$, $p = 0.135$); 6.9% of variation for mist-nets ($df = 5$, $F = 0.3$, $p = 0.614$); for butterflies, 32.5% of variation ($df = 11$, $F = 4.8$, $p = 0.053$) and for amphibians, 40.6% of variation ($df = 7$, $F = 4.1$, $p = 0.089$).

3.5. Relative encounter rates

The highest encounter rate for amphibians, butterflies, understorey birds and nocturnal birds was detected in selectively logged regenerating forest (SLR; see Table 2). Secondary growth forest (CCR) had the highest encounter rates for the overall diurnal bird community and medium-large terrestrial mammals although these were not found to be significantly different. Diurnal transect indicator birds (as listed by Stotz et al., 1996) displayed the highest encounter rate in selectively logged and lowest in secondary forest ($df = 22$, $F = 15.6$, $p = 0.001$; 397 and 173 encounters per 50 km of transect walked respectively). Overall amphibian encounter rates were higher in selectively logged compared to secondary forest ($df = 7$, $F = 8.9$, $p = 0.03$; 212 and 56 encounters per 50 transect nights respectively). Despite showing a trend for higher relative encounter rates in selectively logged forest, the recommended indicator group of amphibians (Strabomantidae; Pearman, 1997) was not statistically different between disturbance areas ($df = 7$, $F = 4.7$, $p = 0.07$). Butterflies displayed the same trend with a higher (non-significant) encounter rate in selectively logged forest ($df = 11$, $F = 3.9$, $p = 0.08$). Mammals, understorey birds and nocturnal birds did not show any differences between habitats ($df = 5$, $F = 0.9$, $p = 0.41$; $df = 22$, $F = 0.4$, $p = 0.55$ and $df = 26$, $F = 2.2$, $p = 0.15$ respectively).

3.6. Community structure

Dominance-diversity plots did not display a standard pattern across all groups (Fig. 3). Butterflies (ΔG=<-0.01, p=<0.001), understorey birds (ΔG=<-0.01, p=<0.001) and nocturnal birds (ΔG=<-0.40, p=<0.01) all showed a more even assemblage

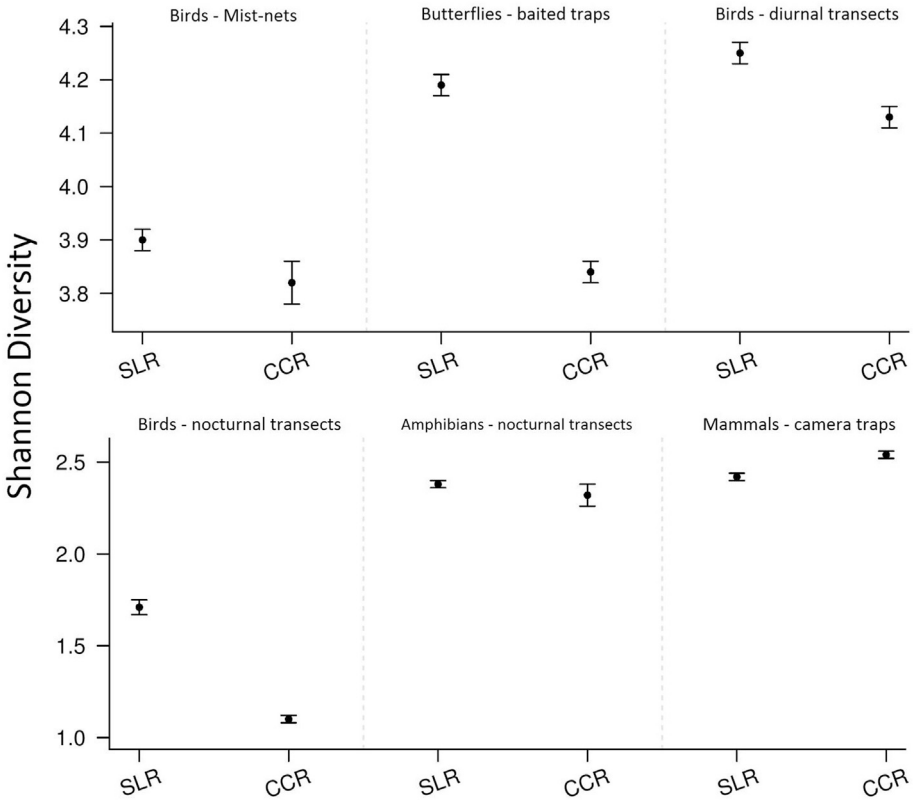

Fig. 2. Shannon species diversity estimates with 95% confidence intervals for study groups across selectively logged (SLR) and secondary growth (CCR) disturbance types.

Table 2
A comparison of relative encounter rate between secondary growth (CCR) and selectively logged (SLR) forests for each study group; p-value relates to an ANOVA test; significance for p-values represent: ** = <0.01 and * = <0.05 and are shown in bold; Strabomantidae is the indicator group of amphibians (Pearman, 1997); bird indicators of good quality habitat for southern Amazonian lowland tropical forest were as indicated by Stotz et al. (1996).

Study group	Measure	Relative encounter rate units	Relative encounter rate		F-statistic $_{df}$ and p-value	R-Sq % (R-Sq adj %)
			SLR	CCR		
Amphibians	Indicator sp	# individuals/50 transect nights	212	56	($F_{1,7} = 4.7$, $p = 0.07$)	43.75 (34.37)
	Overall		**370**	**114**	**($F_{1,7} = 8.9$, $p = 0.03^{*}$)**	**59.59 (52.85)**
Birds - diurnal transects	Indicator sp	# records/50 km of transect walked	**397**	**173**	**($F_{1,22} = 15.6$, $p = 0.001^{***}$)**	**42.58 (39.85)**
	Overall		1090	1320	($F_{1,22} = 2.2$, $p = 0.15$)	9.64 (5.33)
Birds - mistnets	Indicator sp	# individuals/1000 net hrs	46	40	($F_{1,23} = 0.2$, $p = 0.65$)	0.96 (0)
	Overall		384	319	($F_{1,23} = 0.4$, $p = 0.55$)	1.67 (0)
Birds - nocturnal transects	Overall	# records/50 km of transect walked	137	95	($F_{1,26} = 2.2$, $p = 0.15$)	8.19 (4.52)
Butterflies	Overall	# individuals/250 trap days	1327	904	($F_{1,11} = 3.9$, $p = 0.08$)	28.22 (21.04)
Mammals	Overall	# photo captures/50 trap months	343	446	(F1,5 = 0.9, p = 0.41)	17.49 (0)

(regular intervals between species) with more rare species in selectively logged regenerating forest (SLR) than in secondary forest (CCR). However, amphibians ($\Delta G = -0.02$, $p = 0.37$), terrestrial mammals ($\Delta G = -0.02$, $p = 0.30$) and overall diurnal birds (ΔG=<-0.01, $p = 0.54$) showed no statistically significant differences in community structure. Each group showed distinct shifts within community composition in terms of the dominant species between selectively logged and secondary disturbance areas (Fig. 3). For each survey group some of the higher ranked (most abundant) species in selectively logged forest shift to lower ranks and lower encounter rates in secondary forest and in some occasions are not detected at all. The opposite pattern was true for secondary forest, with some of the most dominant species being found in lower encounter rates and representing a lower rank in selectively logged forest.

4. Discussion

Even after decades of regeneration time, and despite a favourable location for recolonization relatively nearby to large protected old-growth forest, our results suggest that the type of anthropogenic disturbance history still affects current biodiversity levels and the patterns of biodiversity distribution of multiple faunal taxa. Locations with a history of complete clearance for agriculture (secondary forest) showed species richness levels 18% (±6.7) lower and species diversity levels 13% (±7.6) lower than historically selectively logged locations; while species encounter rates and community structure also continued to show detectable differences in selected taxa.

Our results apply specifically to the conditions investigated and we should not try to immediately assume other disturbed tropical forests will automatically show patterns of similar magnitude. We therefore suggest that if we are to truly be able to generalise on the causative effect of disturbance history and regeneration on tropical forest biodiversity and conservation value, more direct within site comparisons will need to be investigated. Already this process is underway and our findings on long-lasting differences in Neotropical faunal biodiversity between regenerating selectively logged and secondary forest agree with two recent within-site comparative studies carried out on trees and woody plants in Hainan Island, China (Ding et al., 2017; Xu et al., 2015). Our vegetative surveys displayed similar long lasting differences in dominant tree composition across a site that would have once been similar previous to two different human impacts.

Although previous research has indicated disturbance history to be a key factor driving species richness levels (Ross et al., 2002), we believe that apart from review papers (Bowen et al., 2007; Dunn, 2004) few previous studies (Barlow et al., 2007; Lawton et al., 1998) have directly compared, across multiple taxa, the persistence of biodiversity differences in older regenerating forest (>30 years) in relation to differences in historic human disturbance. For example, the only two (of 34) studies assessed by Dunn (2004) that directly compared more than a single type of forest disturbance, were both carried out on a single taxon, birds (Estrada et al., 1997; Johns, 1991). The same was true for four (of 68) studies that included alternative land uses, assessed by Bowen et al. (2007): ants in the central Amazon (Vasconcelos, 1999), saproxylic beetles in Australia (Grove, 2002), primates in Costa Rica (Sorensen and Fedigan, 2000) and lizards in the Caribbean (Glor et al., 2001). In addition, these studies mostly assessed relatively young regenerating areas (<21 years) and focussed upon comparing the different

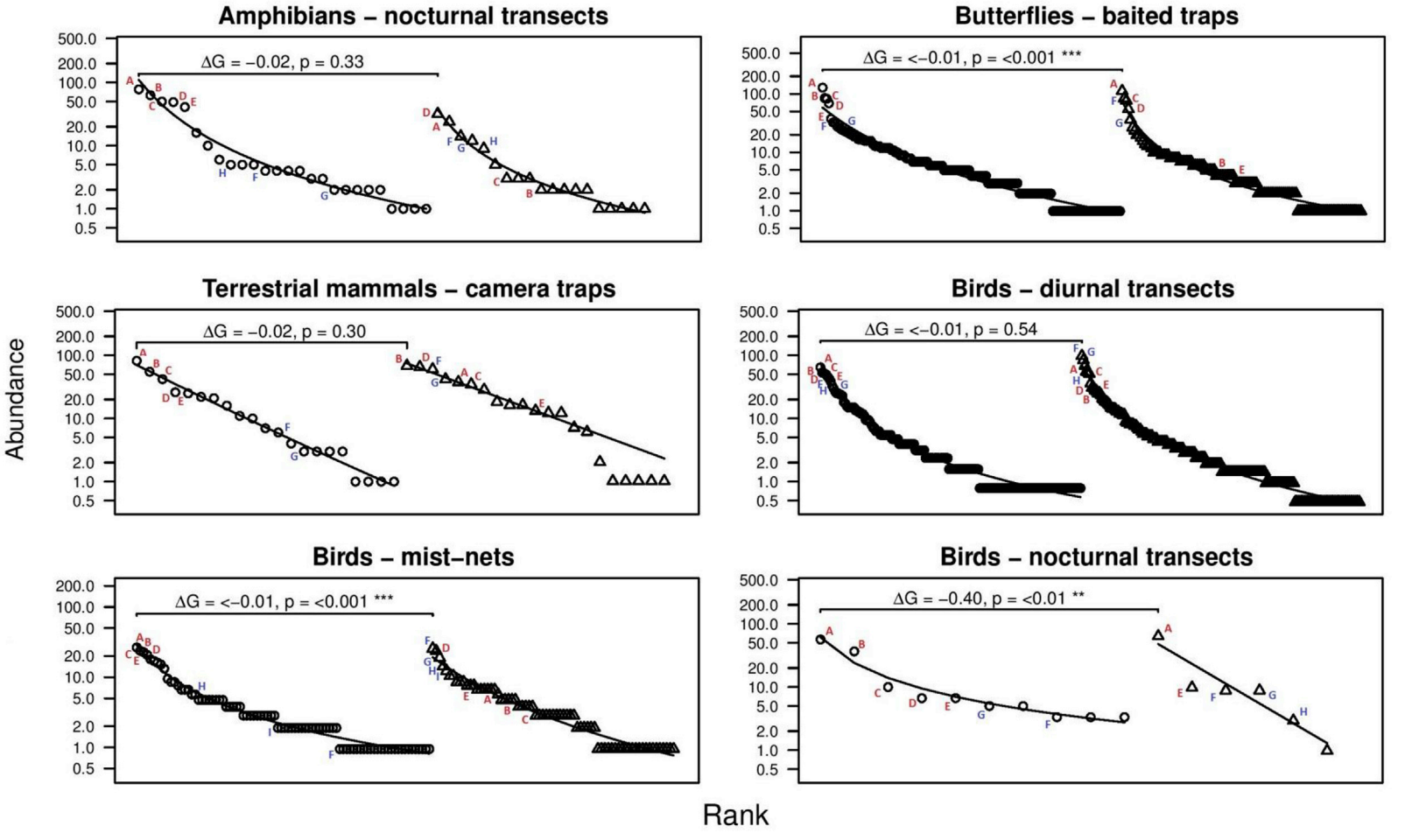

Fig. 3. Dominance diversity (Whittaker) plots for faunal study groups comparing curves for selectively logged (o - left) and secondary growth (Δ - right) disturbance types. For each disturbance history the relative abundance of each species (ni/N) was plotted on a logarithmic scale against the species rank ordered from most to least abundant. Linear models were used to determine if the slopes were significantly different to one another where ΔG denotes to absolute change in gradient and the symbol denote the level of significance of the deviation where *** = ≥0.001, ** = ≥0.01,* = ≥0.05. Points labelled with letters A-E represent the five most abundant species in selectively logged habitat and letters following E represent species from the top five in secondary growth (where different from selectively logged forest).(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

disturbance types with primary forest, as opposed to directly against one another under the same conditions. One such recent assessment between primary and secondary growth forest using the average value approach (focussed on birds), detected a 12% lower species richness in secondary forest than in primary forests (Sayer et al., 2017). Where multi taxon assessments have been carried out (e.g. Barlow et al., 2007; Lawton et al., 1998), they provide indirect comparisons of the biodiversity value of forest with different historic disturbance types because the data are often collected across a variety of landscapes, regions and sites. This is done largely with the aim to provide a greater perspective of the overall landscape, but it can often be complicated to disentangle the effects of disturbance from those of geographic and topographical conditions such as differences in soil types, climatic differences and potential differences in ongoing human difference.

Based largely on such indirect comparisons between biodiversity at different sites, Berry et al. (2010) estimated that on average, 91% (±3.9) of primary forest species are detected in regenerating selectively logged forests. In contrast, Dent and Wright (2009) focussed on regenerating rainforest with different human disturbance histories associated with clearance activities (secondary forest) and categorised sites based on disturbance history into four different prior land-uses. For disturbance histories most similar to the secondary forest in this study, the proportion of primary forest associated species within each area was calculated as follows; pasture or intensive agriculture (46%) and plantation (61%). From these reviews we might therefore have expected the difference between our selectively logged and secondary forest to be at least 30%, and more likely 45% lower, rather than the smaller 18% difference detected here. However, 65 of the 114 (57%) study sites from the review by Dent and Wright (2009) had an age <21 years since abandonment, whereas the findings presented within our study were from forest with over 30 years of regeneration. Had only the 43% of studies with an age >21 years been assessed, then we might expect a value similar to the 18% detected here. Therefore our results along with previous work suggest that even once completely cleared areas have the potential to greatly increase in their biodiversity value given enough time for recolonisation of lost species. If provided with sufficient time for regrowth, and if they are in favourable geographic locations close to old growth areas that can provide source populations, they have the potential to contain levels of biodiversity higher than is often expected based on the average values suggested by previous indirect multi-taxon comparisons.

In addition to the, on average, younger age of regenerating areas assessed previously, what other factors might drive a lower than expected difference between selectively logged forest and secondary post agriculture forest? One possibility is that regenerating forests, such as those studies assessed by Dent and Wright (2009), might be affected by other landscape scale related factors. For example, other secondary forests might not be in such a favourable landscape context for recolonization with less potential for species dispersal and establishment from nearby old-growth forest, or might have been disturbed over a much greater area requiring longer time for recolonization, and therefore might not have regained biodiversity as quickly as in this study. Reduced recolonization potential would also likely mean that the initial post disturbance biodiversity differences between the two different types of recovering forest would remain significantly larger for longer due to the slow recolonization of both areas, and lead to the greater difference detected by Dent and Wright (2009).

Additionally, in this study the close proximity of the different disturbance types allows the potential detection of transient species that can move between forest types at such a scale; but this is likely true for both disturbance types and might have been a greater cause for concern had we detected no difference at all. However, it would be an interesting direction for further research to use longer term data collection to assess how many species are permanently resident in forest following different types of disturbance and how many might simply be transient visitors passing through. In general the study site assessed here is representative of regenerating abandoned lands of the western Amazon and in the Manu Biosphere Reserve in particular; where historic disturbance was typically carried out at a relatively small scale and often located in close proximity to primary forest (Sloan et al., 2015), so our results should be of direct relevance to understanding differences in biodiversity value after disturbance in such conditions.

With the exception of medium-large terrestrial mammals, the taxonomic groups in this study showed a common pattern in species richness and Shannon diversity patterns. The mammals result is perhaps not surprising as previous research has shown that mammals in riverine areas used for ecotourism and areas previously subjected to low-level logging display similar richness levels to primary forest sites (Salvador et al., 2011). These data along with our own results, suggest that medium-large terrestrial mammals may not be useful indicators of different levels of historic anthropogenic disturbance, especially when near to riverine habitat and for larger mobile species over such a small scale. Our results, from a site where animals had been protected from hunting for more than a decade, contrast with those of Burivalova et al. (2014), who found mammals to be the group most sensitive to an increased intensity of logging disturbance. However, Burivalova et al. (2014) acknowledge that although they attempted to exclude studies mentioning current hunting pressures from the meta-analysis, it was possible that hunting was a confounding effect.

In conclusion, in the absence of the confounding effects of on-going disturbance and short regeneration periods, secondary forest within the Manu Biosphere Reserve (and likely other similar forest situated around protected corridors of the western Amazon) has the potential to harbour high levels of biodiversity, albeit lower than those areas only selectively logged. With levels of species richness, diversity, relative abundance and community structures closer to those contained within selectively logged forests than might have previously been predicted from studies dominated by younger areas of regenerating forests, and carried out across different landscapes/regions. We suggest it will be beneficial to investigate further direct within site comparisons of different disturbance histories to determine how widely applicable the effects we have identified will be, and so improve our understanding of the potential value of different types of regenerating rainforest for conservation in specific protected areas. While agreeing with other researchers that preventing further impacts on the world's remaining primary tropical forests is vital in order to sustain the highest levels of biodiversity (Gardner et al., 2007a; Gibson et al., 2011), we

suggest that even following complete clearance, regenerating secondary tropical forests could provide important resources for helping to retain high levels of tropical biodiversity; especially where they remain close to old growth forested areas. In addition to the potential for biodiversity conservation, a median time of 66 years for above-ground biomass to recover to 90% of old-growth values has been suggested for secondary growth forests in the Neotropics (Poorter et al. 2016). This leads us to echo the suggestions of Chazdon et al. (2009a) that preventing further clearance and reconversion to agricultural use of these potentially valuable regenerating landscapes will be an important priority for future biodiversity conservation of the world's tropical forests.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.gecco.2018.e00375.

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